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SOME OBSERVATIONS ON THE CLASSIFICATION OF THE MEMBRACIDAE AND ON THE ANCESTRY, PHYLOGENY AND DISTRIBUTION OF THE JASSOIDEA.

By J. W. Evans, M.A., D.Sc.

(*Commonwealth Institute of Entomology*).

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With 10 Text-figures.

In a recent series of papers (Evans, 1946*a*, *b*, 1947), in which a new basic system of classification was proposed for the many and diverse elements comprised within the jassoid complex, the Jassoidea were divided into five families. Four of these families have already been considered in detail, and the primary purpose of the present paper is to pay some attention to the remaining family, the Membracidae. It is not my intention to attempt to place each separate genus in a definite category, as was done in the case of the other families. I propose merely to draw attention to certain features of the current system of classification of the Membracidae, and at the same time to create two new families for the reception of a few very distinctive genera. In addition the position of the Membracidae, and of the new families, with respect to other jassoid families, will be examined, and the ancestry, phylogeny and distribution of the Jassoidea discussed.

The Classification of the Membracidae.

It is quite certain that wing venation is a remarkably stable character of insects, and if it is correctly interpreted, it provides a valuable guide to relationships. In Part 1 of my *Natural Classification of Leaf-hoppers* I showed how, on the basis of tegminal venation alone, it was possible to separate representatives of the families Aetalionidae, Hylicidae, Eurymelidae and Jassidae.

If an examination is made of the tegmina of a widely representative selection of species comprised in the family Membracidae, at first sight it appears that there is no common basic venational type for the family as a whole. This immediately suggests that the family, as at present understood, is not a homogeneous unit, and further investigation supports this view.

The Membracidae were divided by Stål (1866) into six sub-divisions, and these have been accepted as sub-families by most subsequent workers. They are as follows: Centrotinae, Membracinae, Hoplophorinae, Darninae, Smiliinae and Tragopinae. Haupt, however, recognizes twelve instead of six sub-families, and it is certain that such an increased number is both valid and desirable. His sub-families are the Terentiinae, Centrotinae, Stegaspinae, Tolaniinae, Lampropterinae, Oxyrhachinae, Membracinae, Heteronotinae, Darninae, Polyglyptinae, Hyphinoinae and

Smiliinae. Many of these sub-families he has further split into tribes, thus the Tragopini are reduced to a tribe of the Darninae and the Hoplophorini to a tribe of the Hyphinoinae.

A shortcoming of Haupt's system is that it is incomplete, as several well-defined groups of genera occur which are equally distinctive as those he recognizes as tribes or even sub-families. Nevertheless, it is a marked advance on Stål's classification.

Haupt further divides the Aethalionidae into three sub-families, the Aethalioninae, Ulopinae and Nicomiinae. As *Nicomia* Stål is usually considered as a membracid (e.g. Funkhouser, 1927) it comes within the scope of the present study, but *Ulopa* Fall. is a jassid.

Leaving for the moment further comment on systems of classification, if a search is made within the Membracidae for the most complete and basic type of tegminal venation, and if aberrant forms are neglected, then the type which will be selected will be one similar to that illustrated in fig. 1, A. (*Xiphistes tuberculatus* Walker, South Africa.)

The lettering of the veins in this and in subsequent figures is not in accordance with Funkhouser's (1913) interpretation, since he was of the opinion that in the Membracidae the radius consisted of R_1, R_{2+3} and R_{4+5}, and that the veins, which in my opinion are M_{3+4} and Cu_{1a} were M_{1+2} and M_{3+4} respectively.

Tegminal venation identical with the type illustrated in fig. 1, A occurs also in species in several other genera, as for instance *Oxyrhachis tarandus* F. (India), *Kombazana fidelis* Distant (South Africa), *Oxyrhachidea inermis* Stål (Ceylon) and in *Eufrenchia falcata* Walker (Australia). In Funkhouser's Catalogue of the Membracidae all these genera are included in the Centrotinae, but they are better placed in Haupt's sub-family, the Oxyrhachinae. This sub-family is divided by Haupt into two tribes, the Oxyrhachini and the Centrotypini. While *Oxyrhachis* and related genera merit a separate category, I consider that species in the genus *Centrotypus* Stål are better retained in the Centrotinae.

Some derivations from the basic system of venation are illustrated in fig. 1, B-F and also in figs. 2 and 3. As well as these, numerous examples of secondary specialization also occur, as for instance the reticulate type of venation found in species comprised in the Australian genera *Sextius* Stål and *Goddefroyinella* Distant.

The tegmina illustrated in fig. 1, B-E, all differ from the basic type in having M fused basally with Cu_1 and in having only a single cross-vein, m-cu. The most usual arrangement of veins within the Centrotinae is that shown in fig. 1, B (*Convector cavendus* Distant, India). While forms with such a venation occur more especially in the Oriental, Australian and African regions, a few also occur in the Western Hemisphere (*Marshallella* and *Centriculus* spp.) and in the Palaearctic region (*Acanthophyes* and *Centrotus* spp.).

In the past membracid groupings have been based largely on the shape of the pronotum, but it is clear that the arrangement of the veins of the tegmen offers a more reliable character for the determination of relationships. For example, the venation of *Anchon nodicornis* Germ. (fig. 1, C) is basically identical with that of *Machaerotypus incultus* Melichar (fig. 1, D), but the pattern formed by the arrangement of the veins and the presence of a costal

stigma in the former renders them quite distinct from each other. *A. nodicornis* is from Africa, and in the British Museum there are representatives of no less than fifteen other genera, all also from Africa, which have an identical venational pattern, complete with stigma. *M. incultus* is from Ceylon, and species comprised in seven other genera, all from Ceylon, have the same arrangement of their tegminal veins. It is thus evident that in both instances, while following geographical isolation, changes may have occurred in the shape of the pronotum, meriting not merely specific, but also generic differentiation; the venation of the tegmen has remained substantially the same, and has even retained its intrinsic pattern.

The tegmen of *Microcentrus pileatus* Fowler from Guatemala (fig. 1, D) is unusual, because although m-cu_2 is retained, m-cu_3 is lost, although in the related *Platycentrus acuticornis* Stål from Mexico both m-cu_2 and m-cu_3 are retained. Haupt has removed *Platycentrus* Stål from the CENTROTINAE

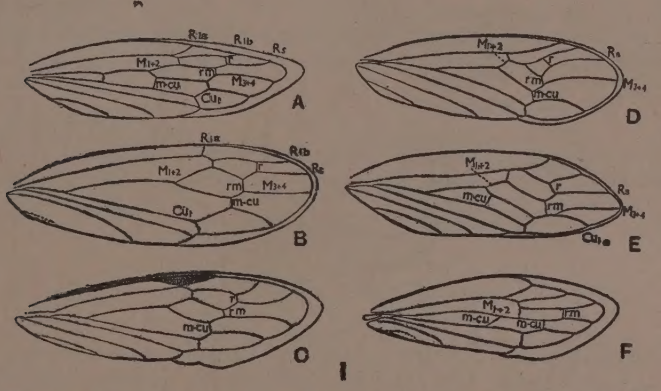

FIG. 1.—Tegmina of A, *Xiphistes tuberculatus*. B, *Convector cavendus*. C, *Anchon nodicornis*. D, *Machaerotypus incultus*. E, *Microcentrus pileatus*. F, *Campylenchia latipes*.

and placed it in the Platycentrini, a tribe of the STEGASPINAE. While I agree that the creation of a separate tribe for the reception of this and related genera is justifiable, in my opinion it would be better placed within the CENTROTINAE.

It is probable that with the exception of two sub-families, the TOLANIINAE and the LAMPROPTERINAE, the leaf-hoppers comprised in the other membracid sub-families of both Stål and Haupt are all derived from the OXYRHACHINAE. This suggestion is based not only on the character of tegminal venation, but also on a balanced analysis of other structural features.

The basic venational system of the MEMBRACINAE is illustrated in fig. 1, F (*Campylenchia latipes* Say, North America). In the tegmen figured not only are M and Cu_1 distinct basally, but M_{1+2} is retained, and the latter feature is unusual in this sub-family. Haupt has divided the MEMBRACINAE into two tribes, the Membracini and the Hypsoprorini, and it is certain that *Hypsoprora* spp., which have reduced venation, are derived from species comprised in genera of the Membracini. The Membracini are confined to the

Western Hemisphere, and are especially well represented in Central and South America.

The HOPLOPHORINAE, which occur only in Central and South America, call for but little comment. Their tegmina invariably lack M_{1+2}, and although in fig. 2, A (*Platycotis histrionica* Stål, Mexico) M and Cu_1 are distinct basally, in other representatives of the sub-family these veins are proximally fused and m-cu_2 is sometimes absent. Haupt does not recognize the HOPLOPHORINAE, but considers the Hoplophorini as a tribe of the HYPHINOINAE, which comprises also the Hyphinoini and the Cymbomorphini. While species contained in the genus *Hyphinoe* Stål are clearly related to *Hoplophora* spp. I prefer to associate *Cymbomorpha* with *Darnis* F., and hence to include it in the DARNINAE as is usually done.

The DARNINAE are a parallel development to the HOPLOPHORINAE and have a similar distribution. The tegmen chosen as representative for this

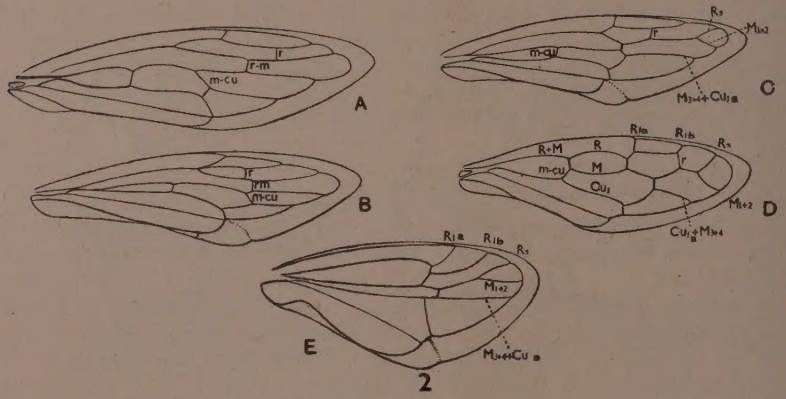

FIG. 2.—Tegmina of A, *Platycotis histrionica*. B, *Stictopelta latilinea*. C, *Telamona cyrtops*. D, *Poppea subrugosa*. E, *Horiola picta*.

sub-family (fig. 2, B, *Stictopelta latilinea* Walker, Brazil) has a venation which is very similar to that of *Platycotis histrionica*, but many of the DARNINAE have M fused for one-third of its length with Cu_1. In most representatives of this group the tegmina when at rest are completely concealed by the pronotum, hence the reduction of the anal area, but in some aberrant forms (e.g. *Hypheus viridistriga* Walker and *Iria carinata* Walker) the tegmina are exposed, and in *H. viridistriga* the venation is reticulate.

Haupt has divided the DARNINAE into two tribes, the Darnini and the Tragopini, but in my opinion the last named group, if not given sub-family status, should then be considered as a tribe of the SMILIINAE.

The SMILIINAE occur in North, South and Central America and their tegminal venation is of particular interest. The Jassoidea almost invariably have four veins supporting the apex of the tegmen. In the EURYMELIDAE these veins are R, M_{1+2}, M_{3+4} and Cu_{1a}; in the HYLICIDAE, R_{1b}, R_s, M_{1+2} and $M_{3+4} + Cu_{1s}$; in the JASSIDAE, R_{1b}, R_s, M_{3+4} and Cu_{1a}. In the SMILIINAE, R_s although fused with M_{1+2} for most of its length (as happens also

in most recent jassid and membracid groups) is distinct apically and the four apical veins are R_{1b}, R_s, M_{1+2} and $M_{3+4} + Cu_{1a}$. The basic type is illustrated in fig. 2, C (*Telamona cyrtops* Fairmaire, North America) and one of the more specialized types of venation in fig. 2, D (*Poppea subrugosa* Fowler, South America). The type of venation exemplified by that of *P. subrugosa* is unique within the MEMBRACIDAE, because, as in the JASSIDAE, R and M are fused basally.

The TRAGOPINAE, which are reduced in size and beetle-like in appearance, have the venation of the tegmen, in its simplest form, identical with the type which is also representative of the SMILIINAE. An example is illustrated in fig. 2, E (*Horiola picta* Stoll, Brazil).

All of Haupt's remaining sub-families occur only in the Western Hemisphere with the exception of the TERENTIINAE, comprising the Terentiini and the Hypsaucheniini. The genus *Terentius* Stål comprises species that are confined to Australia and which lack lateral pronotal processes. They have a tegminal venation similar to the basic type exemplified by *Xiphistes tuberculatus* excepting that m-cu_2 is obselete. *Hypsauchenia* Germ. and related genera occur in the Oriental region. Species in these genera have tall, vertical,

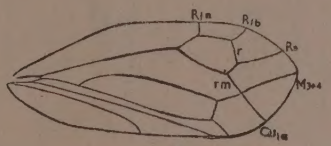

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FIG. 3.—Tegmen of *Stegaspis galeata*.

pronotal processes and a tegminal venation, which, though specialized in some respects, is in essentials also identical with that of *X. tuberculatus*.

The HETERONOTINAE include remarkable ant-like forms, but their tegmina call for no special comment. The POLYGLYPTINAE comprise strange, narrow, ant-like creatures which resemble the SMILIINAE in having R_s and M_{1+2} separate at the apex of the tegmen, and differ from them in having M fused for fully half its length with Cu_1. The STEGASPINAE Haupt has divided into four tribes, the Platycentrini, Stegaspini, Stylocentrini and the Oedini. Apart from *Platycentrus* spp., which I have already suggested are better included in the CENTROTINAE than in the STEGASPINAE, the tegminal venation typical of this sub-family is illustrated in fig. 3 (*Stegaspis galeata* Walker, South America).

The three sub-families which have so far been put on one side must now be considered. These are the LAMPROPTERINAE, the TOLANIINAE and the NICOMIINAE, the last-named being included by Haupt in the AETHALIONIDAE. Goding (1926) regarded the AETHALIONINAE as a sub-family of the MEMBRACIDAE and comprising, in his opinion, the following genera: *Aethalion* Latreille, *Tolania* Stål, *Nicomia* Stål, *Tropidaspis* Stål, *Lophyraspis* Stål, *Lamproptera* Germar, *Stictodepsa* Stål, *Scytodepsa* Stål, *Gerridius* Fowler, *Mina* Walker, *Endoiastus* Fowler, *Eustollia* Goding and *Williamsiana* Goding.

Since in a previous study (1946*b*) I have included only two described

genera, *Aetalion* and *Darthula* Kirk., in the AETALIONIDAE, and still consider that this procedure was correct, alternative groupings are needed for the genera listed above. Some of these have been included by Funkhouser in the CENTROTINAE, but all, I believe, incorrectly. Two of them, *Eustollia* and *Williamsiana*, belong to the JASSIDAE. For the reception of the remainder I am proposing the creation of two new families, one to contain *Nicomia* and *Tolania* and the other for all the remaining genera, and also for the genus *Melizoderes* Blanchard.

NICOMIIDAE.

As a broad descriptive account of the general characteristics of this family might obscure the special features of some of its components, I propose instead to draw attention to a few of the special characteristics of one species, *Nicomia cicadoides* Walker, and then to show in what respects *Tolania* spp. differ from *N. cicadoides*.

In the head of *N. cicadoides* (fig. 4, A) the so-called maxillary suture is retained. This is not a true suture, but the original anterior margin of the

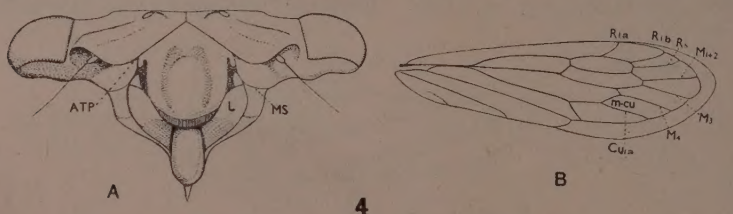

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FIG. 4.—*Nicomia cicadoides*, A, Head, *atp*, anterior tentorial pit; *l*, lorum: *ms*, maxillary suture. B, Tegmen.

head. No trace remains of the epistomal suture, and the epicranial suture forms a wide V. The pronotum, which is extensive and slightly declivous, lacks processes, and the hind margin is transverse. The scutellum, which is completely exposed, is raised antero-medially and has a large flattened, posterior tongue-like extension. The venation of the tegmen (fig. 4, B) is quite unlike that of any other recent jassoid, and recalls the venation of certain Palaeozoic and Mesozoic forms, not only in having more than four veins supporting the apex of the tegmen, but also in the manner in which R, M and Cu_1 approach close together, some distance away from the base of the tegmen, and further in the presence of but a single cross-vein between M and Cu_1.

Species comprised in the genus *Tolania* have certain basic features in common with *Nicomia cicadoides* but they differ in secondary characteristics; thus their heads are posteriorly flattened, and on a plane with the declivous pronotum as far as the antennal ledges. The pronota of *Tolania* spp. differ from that of *N. cicadoides* in having small, or even well developed, lateral horns, but they resemble it in having a similar transverse hind margin. Species in both genera have the scutellum completely exposed and similarly shaped. The venation of the tegmina of *Tolania* spp. is different from that of *N. cicadoides*, since in the former M is fused basally with Cu_1 and M_{1+2} is obsolete;

they resemble it in retaining M_3 and M_4 as separate veins which extend as far as the apex of the tegmen.

Nicomia cicadoides, which was described by Walker in 1862 under the name of *Hoplophora cicadoides*, undoubtedly belongs to Stål's genus *Nicomia*, the type of which is *lemniscata* Stål from Brazil.

Lampropteridae.

This family is created to contain the following genera: *Lamproptera* Germ., *Stictodepsa* Stål, *Scytodepsa* Stål, *Tropidaspis* Stål, *Lophyraspis* Stål, *Gerridius* Fowler (a synonym of *Lophyraspis*), *Mina* Walker, *Endoiastus* Osborn, *Melizoderes* Blanchard and *Orekthen* Funkhouser (a synonym of *Melizoderes*).

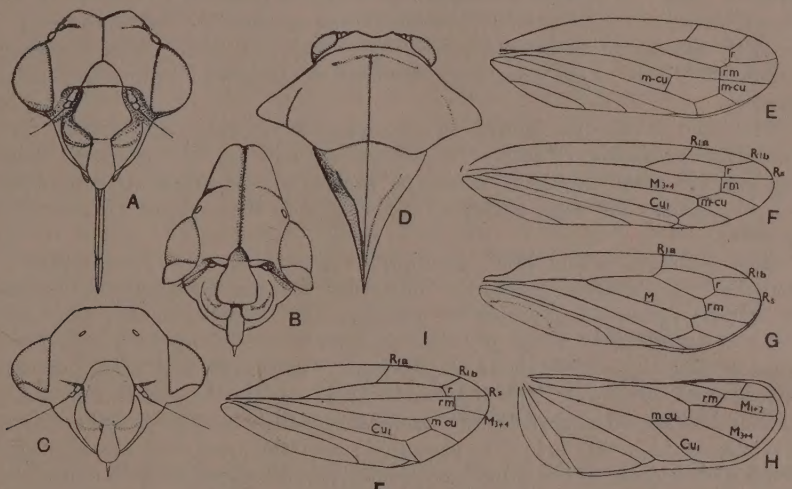

Fig. 5.—A, *Tropidaspis carinata*, head. B, *Endoiastus productus*, head. C, *Lophyraspis armata*, head. D, *Tropidaspis carinata*, head and thorax, dorsal aspect. E, *Melizoderes darwini*, tegmen. F, *Endoiastus productus*, tegmen. G, *Mina aliena*, tegmen. H, *Lophyraspis armata*, wing. I, *Tropidaspis carinata*, tegmen.

Certain features of representatives of some of these genera are illustrated in fig. 5. In head structure, species in this family resemble jassids and aetalionids rather than membracids, and the head is never sharply flexed at the antennal ledges, as is usual, though not universal in the last-named family. The ocelli lie close to the posterior margin of the head, and are distant from the frontal sutures in both *Tropidaspis carinata* F. (fig. 5, A) and in *Endoiastus productus* Osborn (fig. 5, B). This feature recalls the Ulopinae, as do also the deep antennal channels present in the heads of both these species, and as well the wide genae anterior to the eyes in *Endoiastus*. On the other hand the heads of *Melizoderes darwini* Funkhouser and *Lophyraspis armata* Haviland (fig. 5, C) resemble those of certain of the Macropsinae. The vertex of the head of *Mina aliena* Walker is produced into a pair of long lateral horns, and in some species (e.g. *Tropidaspis carinata*, fig. 5, D) the crown, which is,

as it were, the back of the face, projects dorsally above the level of the pronotum.

The pronotum is variously shaped; it may be produced and anteriorly declivous as in *Melizoderes*; wide and apically narrow, as in *Tropidaspis*; raised into a median crest as in *Lophyraspis*; simple and declivous, as in *Mina*, or long and narrow as in *Endoiastus*. The scutellum, which is likewise variable, is always entirely exposed and may be small, or extensive and convex, or raised into a median keel.

The venation of the tegmen is also inconstant in character, but a feature common to the tegmina of all the Lampropteridae is that M is always unbranched, although it may be distinct for its whole length, fused basally with Cu_1, or even fused with R, while in *Lophyraspis armata* R, M and Cu_1 have a common stem. A further characteristic which is common to species in all genera, with the exception of *Melizoderes*, is the absence of cross-vein m-cu_2.

With the exception of *Melizoderes* spp., which occur in Chile, representatives of all the other genera are confined to tropical South and Central America.

Haviland (1925) has figured the egg masses of *Lophyraspis armata* and *Endoiastus productus*. Those of *L. armata* are laid on the surface of twigs and covered with secretions, while the eggs of *E. productus* are embedded in plant tissue. The same author records that both these species are attended by ants.

The illustrations and brief descriptions given above of some representatives of this family may give the impression that the Lampropteridae are an artificial grouping of unrelated genera. This however is not the case, and a balanced study of the principal features of species in the genera *Lamproptera*, *Scytodepsa*, *Stictodepsa*, *Lophyraspis*, *Tropidaspis* and *Mina* discloses that they are all closely related to each other. While the genera *Endoiastus* and *Melizoderes* are more distinctive and less obviously related than the others, they also undoubtedly belong to the same association, and they are of special significance because of the numerous resemblances possessed by their comprised species to jassids in the tribes Ulopini and Macropsini, the two tribes which lie at the base of the jassid stem.

Ancestry and Phylogeny of the Jassoidea.

Already in Lower Permian times there were in existence insects which most certainly belonged to the Homoptera, so it may be assumed that this Order arose during the Carboniferous. Haupt (1929) has claimed that *Blattinopsis reticulata* Germ. from the Upper Carboniferous of Saxony is a true Homopteron, in spite of the fact that the apparently related *B. goldenbergi* Brong. had mandibulate mouthparts. While I consider that the above claim is a mistaken one, I agree that the fore wing of *Recula parva* Schlecht from the same horizon, which Haupt suggests may be that of an insect ancestral to the Cercopidae, is possibly that of an Homopteron.

The only family of Homoptera so far discovered in Lower Permian strata is the Archescytinidae, which Carpenter (1933) has placed in a division, the Palaeorrhyncha, distinct from both the Auchenorrhyncha and the Sternorrhyncha, and which Haupt suggests is directly ancestral to the Jassoidea.

It is conceivable that the ARCHESCYTINIDAE lie close to the line of descent of the Jassoidea, but they cannot possibly have been ancestral to the whole super-family. This is because the media of the tegmen of the ARCHESCYTINIDAE is invariably three-branched, and the common ancester to all the jassoid families must have had a media with four branches. The ARCHESCYTINIDAE differed from recent Jassoidea in having Sc lying close to R for its entire length and in having identical venation in fore and hind wings. Nevertheless their general venational facies is remarkably jassoid-like, and as the long apical abdominal process of *Permoscytina kansasensis* Till. (Carpenter, 1939) suggests affinity with the AETALIONIDAE (because *Darthula hardwickii* Gray has an apparently similar process), it is possible that the ARCHESCYTINIDAE were actually a jassoid family which had already become specialized in certain directions by Lower Permian times.

An amazing abundance of Homopterous remains has been discovered in Upper Permian strata, but before searching among this for ancestral types it will be as well first to recall what features are necessary in any form for it to be acceptable as a possible ancestor to all recent jassoid families.

So far as tegminal venation is concerned these features can be determined if figs. 22–25 in Evans, 1946, are placed beside figs. 1, 4 and 5 in the present paper. An alteration is necessary in the interpretation of venation presented in fig. 22. Formerly I have expressed the opinion that the venation of the tegmen of the AETALIONIDAE differed from that of all other jassoid families in having an unbranched Cu_1. As a result of a further examination of a large number of specimens of *Aetalion* spp., I now consider that I was previously mistaken, and that Cu_1 is two-branched in this family also. The individual variation in the tegminal venation of *Aetalion* spp. is extreme, and it is unusual even to find specimens having an identical arrangement of veins in their left and right tegmina. On this account the point cannot be finally settled until an examination is made of the preceding tracheation of the nymphal wing pads.

In my 1946 paper a reconstruction of the venation of a hypothetical ancestor to the families AETALIONIDAE, HYLICIDAE, EURYMELIDAE and JASSIDAE (fig. 21) was set beside an illustration of the tegmen of *Homaloscytina plana* Tillyard (fig. 20). This tegmen is from the Upper Permian of New South Wales, and the suggestion was made that it possessed most of the features necessary to enable it to be considered as belonging to an insect which could have been ancestral to the four families listed above.

The basic membracid type of tegminal venation (fig. 1, A) closely resembles the jassid type, and differs only in that M is not fused basally with R. The venation of the LAMPROPTERIDAE is reduced and calls for no special comment. That of the NICOMIIDAE as represented by *Nicomia cicadoides*, is, however, of interest because in having but a single cross-vein m-cu and a first cubitus with a proximal bend, it resembles much more the Permian type of homopterous venation than that of other present-day jassoids; at the same time it lacks any features not represented in the tegmen of *H. plana*.

It is thus apparent that the reconstruction (fig. 21, 1946) referred to above applies to all jassoid families, and not merely to the four considered previously.

One feature was omitted in the reconstruction, and this is a transverse nodal line such as occurs in the HYLICIDAE. It is not necessary to suppose

that this line must have been developed in the common ancestor of all jassoid families, but it is an ancient structure, and must have occurred in representatives of an early branch from the principal stem. The suggestion that the tegmen of *H. plana* may be that of a jassoid is, therefore, supported by the occurrence in the Upper Permian of Russia of tegmina with a venation that is basically identical with that of *H. plana*, and which have at the same time a nodal division. Such a tegmen is illustrated in fig. 6 (*Prosbole incerta* B.M.).

Now Haupt and Bekker-Migdisova (1946) believe that the PROSBOLIDAE were ancestral to the Cicadoidea, and the former considers that *Scytinoptera maculata* Mart. was a cercopid, and the latter that the SCYTINOPTERIDAE were a family of the Fulgoroidea.

In my own opinion the tegmina of *S. maculata*, *P. incerta* and *H. plana* were all either those of true jassoids,[1] or else of insects belonging to the stock from which the Jassoidea have been derived. Also, while these particular insects were closely related to the ancestors of both cicadas and cercopids, they were not on the line of descent of the Fulgoroidea.

For the purpose of comparing the SCYTINOPTERIDAE with the Fulgoroidea, abundant tegminal impressions of the former are available, and as well, some

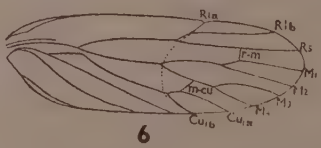

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FIG. 6.—Tegmen of *Prosbole incerta*.

well-preserved fragments of other parts of their bodies. The most striking of these fragments, a head of *Scytinoptera cubitalis* B.M. (1946), is illustrated in fig. 7, B. It is placed for comparison beside that of a recent cixiid, *Achaemenes resurgens* Walker (fig. 7, A). The two heads are entirely dissimilar, and in my opinion, that of *S. cubitalis* does not have a single significant characteristic which might suggest that it had belonged to a fulgoroid. On the other hand it could well be that of an early jassoid, for although no recent jassoid has retained a median ocellus, it is to be expected that one will have been present in their immediate forerunners. If a comparison is made between fig. 7, B and figs. 5, A and B, several resemblances between the scytinopterid and jassoid heads will be evident. For instance, the size and position of the frons, the position of the antennae and the presence of an antennal ledge are features common to all three. In the Fulgoroidea the frons is more extensive, the antennae are differently placed, and there is no ledge overhanging each antenna. So far as the clypeus and the lora are concerned, *S. maculata* again suggests a jassoid, rather than a fulgoroid type.

In the paper by Bekker-Migdisova, from which fig. 7, B has been copied, there are as well several illustrations showing the venation of the tegmen of

[1] The Jassoidea differ from the Cercopoidea and the Cicadoidea in having a reduced tentorium, and if they are of monophyletic origin as is probable, then this cephalic characteristic must have been a very early development, hence an early differentiation of the super-family is to be expected.

Scytinoptera reducta Mart. The venation of this scytinopterid is identical with that of *Homaloscytina plana* in all essential features, the only difference being that in the former, but not in the latter, M_3 is fused with M_4 and the anal veins form a Y-vein. While in all Fulgoroidea the anal veins are distally fused, too much significance should not be ascribed to this character, which is of a secondary nature, and it will be recollected that a Y-vein occurs also in certain jassoids (Stenocotini).

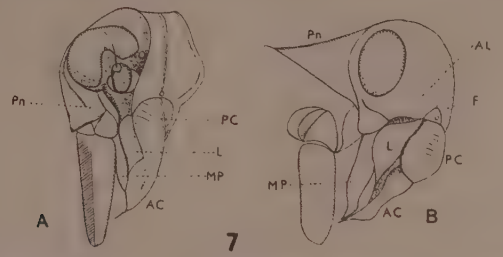

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FIG. 7.—Head and prothorax of A, *Achaemenes resurgens*. B, *Scytinoptera cubitalis* (after Bekker-Migdisova, 1946). *pn*, pronotum; *pc*, post-clypeus; *ac*, anteclypeus; *l*, lorum; *mp*, maxillary plate; *f*, frons; *al*, antennal ledge.

The venation of *Prosbole incerta* is likewise similar to that of *H. plana* and *S. reducta*, and a comparison of fig. 6 with fig. 8, which is an illustration of the tegmen of a cixiid, *Achaemenes resurgens*, will show just how great is the difference between the former and the fulgoroid type of venation. The most obvious difference concerns the subcosta, which in *P. incerta*, if retained at all, is greatly reduced, though in the cixiid it is very well developed.

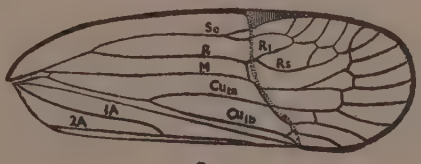

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FIG. 8.—Tegmen of *Achaemenes resurgens*.

While it is easy to refute claims which maintain that the SCYTINOPTERIDAE are a family of the Fulgoroidea, it is less simple to dispose of those which would relate this family to the Cercopoidea.

In most, if not in all recent cercopids, the frons[2] is on the crown of the

[2] Du Porte (1946) and Snodgrass (1947) have pointed out that the frons has no definite anatomical status as the so-called "epicranial suture" has no structural significance. It is in fact merely a line of weakness on the head where the cuticle splits at ecdysis and the arms of the epicranial suture take different courses in different insects. This interpretation is clearly the correct one. Nevertheless the position of the frontal area in Homoptera is constant within limits, and, as the scar of the epicranial split is usually retained to some extent by adult jassoids and is a useful landmark for descriptive purposes, no good reason exists for discarding the use of the term "frons."

head, as shown in fig. 9, D (*Ptyelus flavescens* F.), and not on the face as in *S. cubitalis*. Some tegmina representative of the Cercopoidea are illustrated in figs. 9, A–C. The essential features in which the basic venation of the tegmen of the Cercopoidea differ from the basic jassoid type are the presence in the former of a short Sc, which curves distally towards R, with which it fuses, and in having an unbranched M, which is sometimes secondarily incorporated in part with Cu_1, although always joined basally to the stem of R.

Now Haupt did not consider that the SCYTINOPTERIDAE necessarily belonged to the Cercopoidea but only that *Scytinoptera maculata* Mart. was a cercopid, and it is important to stress this, as the limits of families based largely on tegminal venation are often obscure. The features in which the tegmen of *S. maculata* suggests affinity with the Cercopoidea rather than the Jassoidea are the abbreviated Sc and the absence of m-cu_2.

The venation of the wings of cercopoids differs from those of jassoids, as in the former M is single and Cu_1 has two branches, whereas jassoids have a two-branched M and an unbranched Cu_1. An examination of the wings

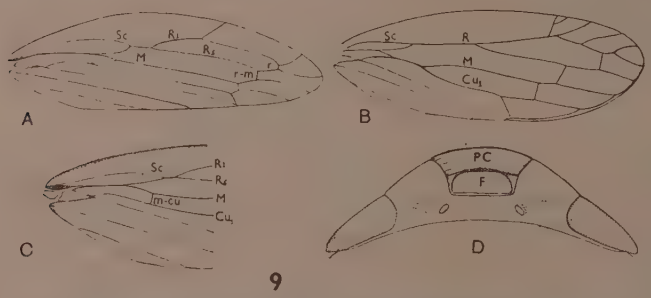

FIG. 9.—A, *Philagra parva* Don., tegmen. B, *Aufidus tripars* Walk., tegmen. C, *Ptyelus flavescens* F., base of tegmen. D, *P. flavescens*, crown of head.

of Permian Homoptera is, however, of no help in indicating particular relationship with any recent group, as they have a media with three branches and a first cubitus with two branches.

While the evidence in favour of the tegmen of *S. maculata* being that of a cercopoid appears unsubstantial and inconclusive, a relationship is probable between some PROSBOLIDAE and cicadas, and I would support Bekker-Migdisova in her suggestion that species in the genus *Tettigarcta* White form a connecting link between Permian forms, such as *Cicadoprosbole soqutensis* B.M. and modern cicadas.

The most striking feature about the known Upper Permian Homopterous fauna is the extreme homogeneity of the venation of the insects represented. With the exception of the PROTOPSYLLIDAE (which are doubtfully Psyllids) it all seems to have belonged to the stock from which the Cicadoidea, Cercopoidea and Jassoidea have arisen, although the head of *Permocicadopsis angustata* Mart. certainly suggests a fulgoroid, and those of *Prosbolopsis* spp. recall the PELORIDIIDAE in having the lora undifferentiated from the clypeus. It is certain that fulgoroids must also have been in existence in Permian times,

and if I am correct in supposing that none of the known remains of Permian Homoptera are those of Fulgoroids, it must be either because they were not preserved in a fossil state, due to the delicacy of their wings, or else because of some environmental factor.

Before passing on to consider the Triassic fauna there are two special structural features of certain Palaeozoic Homoptera which have been preserved in some of their descendants and merit comment. These are the transverse nodal line of the tegmen and the tymbals.

A nodal line as shown in fig. 6 did not occur in all Permian Auchenorrhyncha, but it occurred in several, both in the Russian fauna (e.g. *Cicadoprosbole sogutensis*) and in the New South Wales fauna (e.g. *Austroprosbole maculata* Evans, 1943). At the present time it is a feature of almost all cicadas and is to be found also among the HYLICIDAE. It is developed as well in a modified form in the fore wings of the Heteroptera. In newly emerged adults of the cicada, *Tettigarcta tomentosa* B.W., the tegmen can be readily bent along the axis of the line, but once the wings have dried, they become rigid.

In the Heteroptera generally, in certain cicadas (e.g. *Mogannia* spp. and *Orapa* spp.) and in some Hylicids (e.g. *Balala fulviventris* Walker), the tegmina

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FIG. 10.—Tegminal pad of *Tettigarcta tomentosa*.

either overlap each other apically or they are bent in a ventral direction distal of the nodal line, but in most cicadas and in related groups the tegmina are tectiform, and it is the tectiform condition that is undoubtedly the earlier one.

Cicadas in their nymphal stages are subterranean insects, and Dr. H. E. Hinton has suggested (in conversation) that it would clearly be an advantage to such insects for them to have flexible, rather than rigid, wing pads. Rigid wing pads, especially if they projected at all beyond the sides of the body, would be a hindrance to free movement in a backward direction in the soil. Fig. 10 is an illustration of the wing pad of a pre-imaginal instar of *Tettigarcta tomentosa*. The apical part of the pad, distal of the nodal line, bends inwards towards the abdomen, and the course taken by the line of flexibility would appear to be determined by the effect of the pressure of the pad against the side of the abdomen, together with the transverse position of Cu_{1b}. A similar, though less developed, line of flexibility is shown in the tegmen of *Achaemenes resurgens*, an insect which belongs to a fulgoroid family, the CIXIIDAE, which also has subterranean nymphs.

It might be questioned why, if the nodal line is an adaptation of the nymph to a burrowing life in the soil, it is retained in the adult, when other adaptations to a subterranean existence, such as fossorial forelegs, are not retained. The reason must be that the transverse pressure on the wing pad squeezes the

developing veins and tracheae in such a way that they become swollen on the proximal side of the bend, and the swelling then becomes permanent, as shown in the tegmen of the adult *Tettigarcta tomentosa* (Evans, 1941).

The eggs of cicadas, like those of jassids and some cercopids, are laid in the aerial portions of plants, but while the nymphs of the other groups feed on stem and leaf tissue, those of cicadas, after hatching, drop directly to the ground and feed thereafter on roots. This is an aberrant habit and calls for explanation.

Cicada nymphs are long-lived, and many are probably general rather than specific feeders. Their extended nymphal development period is doubtless the result of the prevailing low temperature of their environment, but it is also conceivable that their surface-living forerunners needed more than a single summer in which to reach the adult stage. The advent of a cold climate would create unfavourable conditions for such insects, and their only chance of survival would lie in seeking the shelter of the soil in which to pass the winter months. This is done by many Holometabola, and Jeannel (1942) has suggested that holometabolism is an adaptation to cold climate conditions. It is thus possible that the subterranean habits of cicada nymphs is a direct result of the late Carboniferous glaciation which occurred in the Southern Hemisphere. A nodal line is present in some Permian Homoptera from Russia, yet Angaraland was never glaciated. However, there is abundant evidence to suggest that the Tethys Sea did not entirely separate the northern land mass from the southern one throughout the Palaeozoic period, and that an exchange of fauna and flora took place.

The other interesting structural features of early Homoptera which have been retained are tymbals. In an earlier paper (1947*a*) I suggested that the Aetalionidae possessed tymbals and that these were homologous with those of cicadas, and Ossiannilsson (1946) claims not only to have found similar structures in various representatives of the Jassoidea, Cercopoidea and Fulgoroidea, but also to have actually heard the " songs " of many of these insects. No trace of tymbals has been recognized in fossil remains, but it can be confidently assumed that such structures must have been present in Carboniferous Homoptera, and were already developed prior to the differentiation of the various separate lines of descent.

Following the Permian and the end of the Palaeozoic era, we come to the Triassic period, and in the Ipswich beds of Queensland which are of this age many well-preserved Homopterous tegmina have been discovered. Among them are some for which Tillyard (1930) created a family, the Ipsviciidae. This family he suggested might foreshadow the Cercopidae, but he placed it in the Fulgoroidea because of the presence of a Y-vein in the clavus. The Ipsviciidae were most certainly not fulgoroids, but may have belonged to the Cercopoidea, as the venation of their tegmina resembles that of recent representatives of this super-family in having Sc retained as a short vein which curves towards R, M reduced to a single vein, and M and Cu_1 amalgamated basally.

Among other representatives of the Ipswich fauna are some remains of insects which Tillyard considered to be jassids and which he named *Eurymelidium australe* Tillyard, *Mesojassus ipsviciensis* Tillyard and *Triassojassus proavittus* Tillyard. All these certainly suggest jassoid relationships, and the

tegmen of *E. australe* might even be that of a eurymelid as it lacks Rs and has a two-branched media.

Of the limited Homopterous remains of Jurassic age, the tegmen of *Jassites punctatus* Brodie (figured by Handlirsch, 1908) almost certainly had belonged to a jassid (as apart from a jassoid), as had also the tegmen of *Mesojassoides gigantea* Oman (1937) from the Cretaceous of Colorado and the Eocene *Maleojassus primitivus* Zeuner (1941) from the Isle of Mull.

Distribution.

The available evidence would seem to suggest that either true jassoids, or else their immediate ancestors, were in existence during the Permian. In Triassic strata tegmina have been found which are undoubtedly those of jassoids. The passing of the Palaeozoic flora will have been accompanied by most of the associated fauna, and it is probable that of the Mesozoic Homopterous fauna but little survived into the Tertiary. Nevertheless it is possible that the families Aetalionidae, Hylicidae and Nicomiidae were already differentiated by Triassic times, and that the stock from which the Eurymelidae were later to develop was also in existence during this period. On the other hand the Lampropteridae, Membracidae and Jassidae probably did not diverge along separate lines of evolution until a later date.

The rise and spread of the family Jassidae, as apart from the Jassoidea, is doubtlessly linked with the development and dispersal of Angiosperms; thus it cannot have taken place earlier than the Cretaceous. At the same time the fossil evidence, meagre though it is for the whole of the Mesozoic era, would seem to indicate that jassids were differentiated either before, or else during, the Jurassic. Some supporting evidence for this possibility is found in the fact that an undoubtedly ancient jassid, *Koebelia californica* Baker, feeds on pines in California, and not on Angiosperms, and also in the present distribution of the more ancient groups.

Metcalf (1946), in a discussion of the inter-relationships between genera and zoogeographic regions, has pointed out that the Homoptera are especially valuable as geographic indices because for the most part species are limited to a single host plant, or to a narrow range of plants, and many of them are insects of relatively small size without strong powers of flight.

The literature associated with the intriguing subject of former land connections is at present conflicting. For this reason it is essential that all those who have special evidence of any sort to contribute should make it available, in order that one day a comprehensive and balanced analysis may be written.

In earlier papers I have made mention of the distribution of the various jassoid groups, and here intend merely to recapitulate the principal features of their geographical occurrence, and to draw attention to a few significant points.

Hylicidae.

This family must have been already in existence prior to the first separation of Australia from Asia, and before Northern Africa lost contact with Northern South America. Nevertheless although now occurring in China, Southern India and Tropical Africa, it is absent from both Australia and South America.

This absence could be due to unfavourable environmental factors in Australia and South America, but another explanation might be that the HYLICIDAE formed part of the ancient fauna of Angaraland,[3] and did not spread to India until after contact was lost with Australia and the sea had separated Africa from the South American continent.

EURYMELIDAE.

This family is confined to Australia, New Guinea and New Caledonia. The most recently evolved sub-families, the EURYMELINAE and the POGONOSCOPINAE, are associated especially with eucalypts, and their genera and species will have been segregated during middle and late Tertiary times. The third sub-family, the IPOINAE, has a wider range of food-plants, and while some of its genera will have been contemporaneous with those of the EURYMELINAE (e.g. *Ipo* Kirkaldy), others are of more ancient origin. These latter may be survivors from the Cretaceous or even earlier periods.

With but a single exception (*Eurymeloides nigra* Evans) all the EURYMELIDAE so far recorded from New Guinea are closely related to Australian forms, and will have reached New Guinea not earlier than Pliocene times. Only a single eurymelid has been described from New Caledonia; this species, *Ipoides leai* Evans, belongs to a genus which has also several Australian representatives.

NICOMIDAE.

It is possible that representatives of this small tropical American family are but little changed from their forerunners which may have existed in Triassic times.

AETALIONIDAE.

Representatives of the AETALIONIDAE now occur only in South-west India and in tropical America. Their former distribution must have been more extensive, and they will certainly at one time have inhabited parts of Africa.

LAMPROPTERIDAE.

The LAMPROPTERIDAE, which may be derived from the AETALIONIDAE, and which lie close to the stem from which both the MEMBRACIDAE and the JASSIDAE arose, occur, apart from one genus in Chile, only in Tropical America.

MEMBRACIDAE.

The oldest sub-families of the MEMBRACIDAE, the OXYRHACHINAE and the CENTROTINAE, are most abundant as to genera and species in the Oriental region. These sub-families also have numerous representatives in Africa and Australia, and a few in Europe and the Americas. They must already have been in existence prior to the first separation of Australia from Asia,

[3] Angaraland corresponds to Mongolia and adjacent parts of Siberia and China, and is considered by geologists not only to have persisted as a land mass since Cambrian times, but also never to have been glaciated.

and before Africa lost contact with northern South America. The remaining sub-families of the MEMBRACIDAE, apart from the TERENTIINAE (which occur in the Oriental and Australian regions), are confined to the Nearctic and Neotropical regions, being especially well represented in the latter region. They are all derivatives of the OXYRHACHINAE and CENTROTINAE, and must have evolved during Tertiary times.

JASSIDAE.

In Part 3 of my *Natural Classification of Leaf-hoppers* a table was given (p. 107) showing the essential features of Jassid distribution. In this table forty-two separate groups were arranged in a presumed evolutionary sequence and also in terms of their distribution. In this paper I suggested that the ULOPINAE and the MACROPSINAE may lie close to the base of two separate lines of jassid descent, and it is interesting to find that both these groups are especially associated with the old southern continent, and must already have been in existence when Southern Africa, Australia, New Zealand and southern South America all formed part of a single land mass.

The evidence on which this surmise is based is as follows: the Ulopini, some of which are associated more with a particular micro-environment than with a specific host-plant, although occurring also in Europe, Asia and North Africa, are especially well represented in South Africa, Australia (particularly Tasmania) and New Zealand. The Cephalelini, which are specialized derivatives of the Ulopini, occur only in South Africa, Australia (especially S.W. Australia and Tasmania) and New Zealand.

The Macropsini now have a universal distribution, but those species which retain the most primitive characteristics (and in certain features approach close to the LAMPROPTERIDAE) are restricted to Western Australia. Many Western Australian forms show close affinity to others that occur in South Africa; an undescribed New Zealand species of *Macropsis* feeds on *Nothofagus*, an Antarctic tree, and the genus of the LAMPROPTERIDAE closest to *Macropsis* Lewis (*Melizoderes*) occurs in Chile.

Apart from certain forms of restricted distribution, the next most ancient groups of jassids are apparently the Ledrini and the NIRVANINAE, both of which extend across the tropics from Australia to Central America and occur intermediately in India and Africa. They are but sparsely represented in the Western Hemisphere and probably were originally of Oriental provenance. The Krisnini, a tribe of the JASSINAE, resembles the OXYRHACHINAE and CENTROTINAE in the MEMBRACIDAE in having achieved a new evolutionary impetus on arrival in America. Representatives of the actual tribe occur only in India, Africa and Costa Rica, but their apparent derivatives, the Gyponini, comprise a large number of genera and species, all of which are confined to the Americas.

Next in time come a few groups, such as the Signoretini, which occur only in the tropics of Asia and Africa, and those numerous ones which arose as a result of long geographical isolation during the Tertiary, as for instance the MELICHARELLINAE in the Eremian sub-zone and the AUSTROAGALLOIDINAE in Australia. Some others, which may be approximately contemporaneous with the above, give evidence of various former land connections, for example

the Thymbrini (Australia and New Zealand ; Erhomenellini (W. Europe and N. America) ; Dorycephalini (E. Europe and N. America) ; Eupelicini (Europe, N. Africa, Canary Islands).

The two most recent and widespread groups of jassids, which I have formerly suggested represent the culmination of the development of the Ulopides and Macropsides, are the TETTIGELLINAE and the EUSCELINAE. Of these, the former is now best represented in tropical America, and the latter in North America and Europe.

Uvarov (1930) has suggested that the marsh-haunting habits of some British Orthoptera are associated with the fact that they are of tropical origin. It is significant therefore that the sole indigenous European representative of the TETTIGELLINAE, *Tettigella viridis* L. (which occurs also in Japan), " is abundant in damp grassy places " (Edwards, 1896), and that the three Tasmanian species of *Tettigella* also occur only in a marsh environment. The latter are closely related to others which inhabit New South Wales, Queensland and Japan, and very probably reached the southernmost extremity of Australia during the pluvial period, that either accompanied or else immediately preceded the Pleistocene glaciation. It is conceivable that it was during the same pluvial period that the hygrophilous PELORIDIIDAE (Coleorrhyncha) extended their range of distribution as far northward as Southern Queensland.

The EUSCELINAE will almost certainly also have reached Australia from the North during late Tertiary times, and it is quite possible that some may have come from the west by way of the Oriental region, and others have travelled around the margin of the Pacific from the east.

ACKNOWLEDGMENTS.

My thanks, as usual, are due to Dr. W. E. China for the benefit of his help and advice, which have always been freely given when sought.

REFERENCES.

BEKKER-MIGDISOVA, H. E., 1946, Contributions to the knowledge of the comparative morphology of recent and Permian Homoptera. *Bull. Acad. Sci. U.R.S.S.* **6** : 741.

——, 1947, *Cicadoprosbole sogutensis* B.M., a transitional form between the Permian PROSBOLIDAE and modern cicadas. *Doklady Acad. Sci. U.R.S.S.* **55** : 445.

CARPENTER, F. M., 1933, The Lower Permian insects of Kansas, Pt. 6. *Proc. Amer. Acad. Arts Sci.* **68** : 411.

——, 1939, The Lower Permian insects of Kansas. *Ibid.* **73** : 29.

DU PORTE, E. M., 1946, Observations on the morphology of the face in insects. *J. Morph.* **79** : 371.

EVANS, J. W., 1941, The morphology of *Tettigarcta tomentosa* White. *Pap. R. Soc Tasm.* **1940** : 35.

——, 1943, Upper Permian Homoptera from New South Wales. *Rec. Aust. Mus.* **21** : 180.

——, 1946*a*, A Natural Classification of Leaf-hoppers, Pt. 1. *Trans. R. ent. Soc. Lond.* **96** : 47.

——, 1946*b*, A natural classification of leaf-hoppers, Pt. 2. *Ibid.* **97** : 39.

——, 1947 A natural classification of leaf-hoppers, Pt. 3. *Ibid.* **98** : 105.

FUNKHOUSER, W. D., 1913, Homologies of the wing veins of the MEMBRACIDAE. *Ann. ent. Soc. Amer.* **6** : 74.

——, 1927, *General Catalogue of Hemiptera* Fasc. 1, MEMBRACIDAE.

GODING, F. W., 1926, A classification of the MEMBRACIDAE of America. *J. N.Y. ent. Soc.* **34** : 207.

HANDLIRSCH, A., 1908, *Die Fossilen Insekten*. Leipzig.

HAUPT, H., 1929, Neueinteilung der Homoptera-Cicadina nach phylogenetisch zu-wertenden Merkmalen. *Zool. Jb.* (*Syst.*) **58** : 173.

HAVILAND, M. D., 1925, The MEMBRACIDAE of the Kartabo Bartica District, British Guiana. *Zoologica* **6** : 229.

JEANNEL, R., 1942, *La Genèse des Faunes Terrestres*. Paris.

METCALF, Z. P., 1946, The center of origin theory. *J. Elisha Mitchell Sci. Soc.* **62** : 149.

OMAN, P. W., 1937, Fossil Hemiptera from the Fox Hills Sandstone of Colorado. *J. Palaeont.* **11** : 38.

OSSIANNILSSON, F., 1946, On sound production and the sound-producing organ in Swedish Homoptera-Auchenorhyncha. *Opusc. ent.* **1946** : 82.

SNODGRASS, R. E., 1947, The insect cranium and the " epicranial suture." *Smithson. misc. Coll.* **107** : (7).

STÅL, C., 1866, *Hemiptera Africana* **4** : 82.

TILLYARD, R. J., 1920, Mesozoic insects of Queensland, No. 7, Homoptera. *Proc. Linn. Soc. N.S.W.* **44** : 857.

UVAROV, B. P., 1930, Contribution a l'étude du Peuplement des Iles Britanniques. Orthoptera. *Soc. Biogr.* **3** : 57.

WALKER, F., 1862, Characters of undescribed species of Homoptera in the collection of F. P. Pascoe. *J. ent.* **1** : 317.

ZEUNER, F. E., 1941, The Eocene insects of the Ardtun Beds, Isle of Mull, Scotland. *Ann. Mag. nat. Hist.* (11) **7** : 82.